

# Biogeography of Braconid Parasitoids of the Caribbean Fruit Fly (Diptera: Tephritidae) in Florida

AVI EITAM,<sup>1</sup> JOHN SIVINSKI,<sup>2,3</sup> TIM HOLLER,<sup>4</sup> AND MARTIN ALUJA<sup>5</sup>

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**ABSTRACT** The geographic distribution of three braconid parasitoids of the Caribbean fruit fly, *Anastrepha suspensa* (Loew), was determined by collecting host fruit throughout central and southern Florida. *Diachasmimorpha longicaudata* (Ashmead) was most abundant in southern Florida, occurring at higher latitudes along the Atlantic and Gulf coasts. Distribution of this species was negatively related to variance of monthly temperatures. This suggests that *D. longicaudata* may be dependent on a relatively constant supply of hosts. *Doryctobracon areolatus* (Szepligeti) was the dominant species at the majority of interior locations, but it was uncommon or absent along both coasts. *Utetes anastrephae* (Viereck) was widespread but usually less common than the other species. Parasitism levels of both *D. areolatus* and *D. longicaudata* were positively related to density of common guava, *Psidium guajava* L., trees. Parasitism levels of both *D. longicaudata* and *U. anastrephae* were positively related to numbers of *A. suspensa* captured in McPhail traps. Abundance of *D. areolatus* was inversely related to that of both *D. longicaudata* and *U. anastrephae*. The absence of *D. areolatus* in southeastern Florida, where it was originally established, suggests that a process of competitive displacement may have occurred. Parasitoid distribution is consistent with the hypothesis that *D. areolatus* is a superior searcher and *D. longicaudata* is a superior intrinsic competitor.

**KEY WORDS** Braconidae, distribution, environmental factors, interspecific competition

DISTRIBUTION MAY BE AFFECTED by a variety of environmental factors. For parasitoids in general, and for parasitoids of tephritid fruit flies in particular, these factors may be abiotic (such as temperature and precipitation) and biotic (such as the distribution and abundance of hosts and interspecific competition). Temperatures may be critical in limiting distribution of tropical species at high latitudes. Snowball and Lukins (1964) suggest that low winter temperatures limit the distribution of the braconid *Fopius* (formerly *Bios-teres*) *arisanus* (Sonan) in southern Australia. Darby and Kapp (1934) reported that tolerance of low temperatures by the braconid *Doryctobracon crawfordi* (Viereck) is less than that of its tephritid host *Anastrepha ludens* (Loew).

Host fruit availability has a major effect on distribution and abundance of tropical tephritids, including the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Vargas et al. 1983, 1989, 1990; Tan and Serit 1994); the melon fly, *Bactrocera cucurbitae* (Coquillett) (Harris et al. 1986; Harris and Lee 1989; Vargas et al. 1989, 1990);

and *Anastrepha* spp. (Malavasi and Morgante 1981, Fehn 1982, Malo et al. 1987, Celedonio-Hurtado et al. 1995) and may similarly influence parasitoid abundance (Vargas et al. 1993). Parasitoids may be influenced by the temporal dynamics of their hosts. Fruit yield can be adversely affected by temperatures or rainfall that is periodically higher or lower than optimal (Raper and Kramer 1983, Petr 1991). Consequently, high variance in these abiotic factors would lead to high variance in the temporal availability of hosts. Parasitoid species may differ in their ability to survive periods of low host abundance, and their persistence in a geographical region could therefore be indirectly related to the variance in abiotic factors.

Finally, interspecific competition may be a critical determinant of parasitoid distribution. Competitive displacement has been suggested as the reason for the decline or disappearance of populations of fruit fly parasitoids in two separate cases in Hawaii (Pember-ton and Willard 1918, van den Bosch and Haramoto 1953). Likewise, competitive displacement of aphid parasitoids has been reported from the continental United States (Murdoch et al. 1996, Schellhorn et al. 2002).

The Caribbean fruit fly, *Anastrepha suspensa* (Loew), became established in Florida in 1965 and quickly spread throughout southern and central Florida (Weems 1966). In an effort to control it, several species of parasitoids were introduced to the state (Baranowski et al. 1993). The first to be released was *Doryctobracon areolatus*

<sup>1</sup> Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611 (e-mail: eitam@yahoo.com).

<sup>2</sup> Center for Medical, Agricultural and Veterinary Entomology, USDA-ARS, P.O. Box 14565, Gainesville, FL 32604.

<sup>3</sup> Corresponding author, e-mail: jsivinski@gainesville.usda.ufl.edu.

<sup>4</sup> USDA-APHIS-PPQ-CPHST, Gainesville Plant Protection Station, P.O. Box 14565, Gainesville, FL 32604.

<sup>5</sup> Instituto de Ecología, A.C., Apartado Postal 63, 91000 Xalapa, Veracruz, Mexico.

(Szepligeti) [= *Parachasma cereus* (Szepligeti)] (Hymenoptera: Braconidae: Opiinae) (Baranowski and Swanson 1970). This is a widespread larval-pupal parasitoid, ranging from Mexico to Argentina (Wharton and Marsh 1978). An original stock of seven males and 17 females from Trinidad was reared through six to seven generations, and 45 males and 26 females were released at Homestead, FL, in 1969 (Baranowski et al. 1993). Although it was recovered in large numbers the next summer, populations at this site have since declined (Baranowski et al. 1993). Small numbers persisted in the area, at least until the occurrence of Hurricane Andrew in 1992 (Sivinski 1991).

*Diachasmimorpha longicaudata* (Ashmead), another larval-pupal opine braconid, was introduced to Florida in 1972. This Indo-Philippine species, originally recovered from *Bactrocera* spp., has been used in the biological control of a wide range of tephritid hosts in various regions of the world (Clausen 1978). In contrast to the limited release of *D. areolatus*, *D. longicaudata* was released in large numbers in 21 counties throughout central and southern Florida (Baranowski et al. 1993). Based on reduced fly catches in subsequent years, it seemed to have had a significant effect upon host fly populations (Baranowski et al. 1993, Sivinski et al. 1996).

Two other exotic larval-pupal parasitoids, *Acerato-neuromyia indica* Silvestri (Hymenoptera: Eulophidae) and *Trybliographa daci* Weld (Hymenoptera: Figitidae: Eucosilinae), also have been established (Baranowski et al. 1993); however, they are rarely collected. In addition, two native larval-pupal braconid parasitoids, *Utetes anastrephae* (Viereck) and *Doryctobracon anastrephilum* (Marsh), originally parasitoids of *Anastrepha interrupta* Stone in extreme southern Florida, were recovered from *A. suspensa* in small numbers before the introduction of the exotic species (Baranowski et al. 1993). Like *D. areolatus*, *U. anastrephae* has a wide distribution and is found as far south as Argentina (Wharton and Marsh 1978).

Previous studies indicated that abundance of *A. suspensa* parasitoids varied among locations in Florida. Sivinski et al. (1996) reported that *D. areolatus* was the dominant parasitoid in areas west of Lake Okeechobee. However, it was absent from their samples in southeastern Florida. Intensive fruit sampling along the central Atlantic coast during 1993–1994 confirmed the presence of many *D. longicaudata* and *U. anastrephae*, but few *D. areolatus* (Denise Marshall, personal communication).

In this study, we determine the distribution of parasitoids throughout central and southern Florida and identify abiotic and biotic factors that may influence this distribution. We relate the relationships among parasitoid species on this large geographic scale with those found in previous studies on local (within tree canopies) and regional scales.

### Materials and Methods

**Fruit Sampling.** We collected host fruits of *A. suspensa* in 23 towns in central and southern Florida (Fig.

1), chosen to represent various regions of the peninsula: five sites along the Atlantic coast from Melbourne (28.1° N) to Miami (25.8° N), seven sites along the Gulf of Mexico coast from Tampa (28.0° N) to Naples (26.1° N), and 11 sites in the interior from Dade City (28.4° N) to Belle Glade (26.7° N) and LaBelle (26.8° N). Clewiston, on the southwestern coast of Lake Okeechobee, and Immokalee, 37 km south of LaBelle, were not sampled because of previous mass releases of *D. longicaudata* at these locations (Sivinski et al. 1996). There are only very small interior towns south of those indicated due to the presence of the Everglades, an extensive swamp and marsh region that is generally free of *A. suspensa* hosts.

We sampled at Ft. Pierce in March and May 1993, before augmentative releases of *D. longicaudata* in that region (Burns et al. 1996) and at all other sites in August 1994 and monthly from January to September 1995, depending on fruit availability. Due to low sample numbers in 1994 and 1995, we collected additional samples monthly at Melbourne, Bradenton, Venice, and Okeechobee from March to May 1996 and at St. Petersburg in May 1996. We did not sample from October through December because at most sites, primary *A. suspensa* host fruits are uncommon during this period in most years (T.H., unpublished data). All samples were collected within a single week each month.

Fruits sampled included loquat, *Eriobotrya japonica* (Thunb.); Surinam cherry, *Eugenia uniflora* L.; Cattley guava, *Psidium cattleianum* Sabine; and common guava, *Psidium guajava* L. Loquat samples were collected from January to April, most Surinam cherry samples from April to June, most Cattley guava from July to August, and most common guava from August to September. Additional fruiting periods may occur, especially at southern sites. Total number of samples ranged from 17 at Ft. Pierce to 102 at LaBelle (Table 1), depending primarily on availability of host fruit; up to 12 samples were collected per site during a single month. Loquat was the most commonly collected fruit with 549 samples, compared with 377, 83, and 290 samples of Surinam cherry, Cattley guava, and common guava, respectively (Table 2). Each sample included fruits collected from a single tree (means of 30, 61, 30, and six fruits per tree for loquat, Surinam cherry, Cattley guava, and common guava, respectively). Fruits collected were ripe and usually without holes caused by beetles or exiting larvae. They were preferably collected from the tree but occasionally supplemented with fruits from the ground.

After collection, we placed the fruits upon a metal screen within a bucket. The buckets had holes for ventilation and were covered with a plastic lid. Their insides were lined with cloth to prevent entry of insects after fruit collection and the escape of insects emerging from the fruit sample. Moist fine vermiculite ( $\approx 15$  ml water per 100 cm<sup>3</sup> of vermiculite) was placed at the bottom of the bucket. Mature fruit fly larvae exited the fruit and pupated in the vermiculite.

At the end of each sampling week, we collected the buckets from various locations and transported them

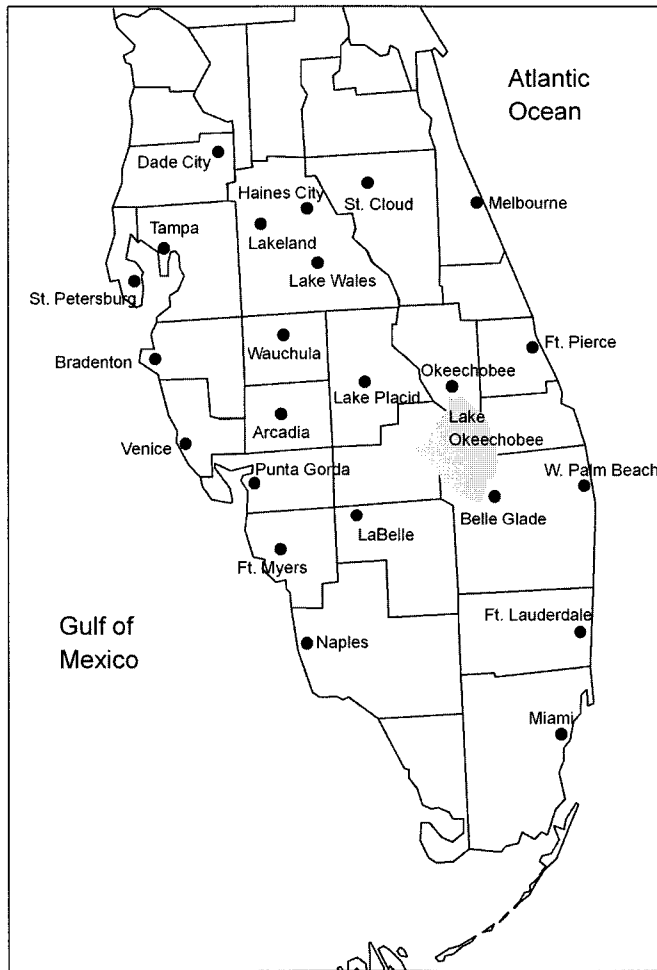


Fig. 1. Fruit sample collection sites.

to Gainesville. Buckets were maintained at 25.5°C, except in 1995 when they were kept in a warehouse at ambient temperatures. We sifted the puparia from the vermiculite 13–15 d after fruit collection and transferred them to fresh vermiculite in 250-ml plastic containers. These containers were initially covered with a solid lid, which was replaced after  $\approx 1$  wk with a screened lid. This was done to ensure that the vermiculite did not dry out but was not so moist as to promote development of fungi. Containers were maintained at 25.5°C and ambient humidity.

Flies and parasitoids emerged within the containers and were counted when no more live insects were observed. Parasitism levels for each species were calculated for each sample as the ratio between the number of parasitoids of the relevant species emerging and the sum of all flies and parasitoids emerging. This assumes that neither the flies nor the parasitoids diapause and that mortality levels of the fly pupae and immature parasitoids are similar. In Florida, typically,  $\approx 90\%$  of pupae held indoors under controlled temperature and humidity produce adults (J.S., unpub-

lished data), so it is unlikely that a significant proportion of parasitoids undergo diapause. In contrast, diapause seemed to be quite prevalent among parasitoids held under seminatural conditions in Mexico (Aluja et al. 1998). True levels of parasitism are likely underestimated because fruit removed from the field include host eggs and larvae that might later have been parasitized if left in place; however, comparisons of parasitism levels as measured should reflect relative abundance.

**Abiotic Environmental Data.** We obtained temperature and precipitation data from the Southeast Regional Climate Center, Columbia, SC. Weather stations exist in most of the towns included in the study. However, no data are available for the vicinity of Dade City and Haines City. Data from Winter Haven and Avon Park were used to represent Lake Wales and Lake Placid, respectively. The following variables were obtained: mean annual temperature, mean minimum temperature for the coldest month of the year, mean maximum temperature for the warmest month

Table 1. Numbers of samples collected and insects emerging for various sites

Site	No. samples <sup>a</sup>					No. insects emerging			
	Total	with CFF	with Da	with Dl	with Ua	CFF	Da	Dl	Ua
Arcadia	59	57	27	0	1	3,095	589	0	3
Belle Glade	71	63	0	20	9	3,462	0	106	27
Bradenton	64	48	0	1	4	1,816	0	6	33
Dade City	35	32	0	0	0	672	0	0	0
Ft. Lauderdale	54	48	0	12	9	2,746	0	214	59
Ft. Myers	65	59	9	22	19	3,092	27	156	79
Ft. Pierce	17	17	0	7	8	1,352	0	10	110
Haines City	31	18	1	0	0	281	1	0	0
LaBelle	102	95	42	43	2	3,267	768	482	7
Lakeland	81	63	13	0	1	3,629	172	0	2
Lake Placid	70	64	23	0	1	2,837	356	0	1
Lake Wales	67	59	19	0	0	2,500	230	0	0
Melbourne	84	53	0	0	0	961	0	0	0
Miami	48	40	0	11	4	2,539	0	81	10
Naples	76	49	2	9	6	1,210	5	58	36
Okeechobee	46	40	6	4	1	1,748	181	9	7
Punta Gorda	54	36	5	1	3	1,479	19	1	11
St. Cloud	49	37	0	0	2	1,288	0	0	16
St. Petersburg	50	34	0	0	0	1,354	0	0	0
Tampa	37	28	2	0	0	1,198	2	0	0
Venice	35	31	1	0	13	2,097	1	0	60
Wauchula	79	75	36	0	3	4,368	599	0	16
W. Palm Beach	25	19	0	3	1	439	0	51	5

CFF, Caribbean fruit fly; Da, *Doryctobracon areolatus*; Dl, *Diachasmimorpha longicaudata*; and Ua, *Utetes anastrephae*.  
<sup>a</sup> Each sample includes fruits from a single host tree.

of the year, extreme annual minimum and maximum temperatures, and annual precipitation.

We calculated the annual variance of the following monthly values: mean temperature, mean minimum temperature, mean maximum temperature, extreme minimum temperature, extreme maximum temperature, and precipitation. Variance in these values reflects seasonality. For all variables, the mean value for the years 1980–1996 was used for analysis.

**Host Plant and Host Fly Data.** We performed a survey to estimate the relative density of host fruit trees for various towns. Quadrants were chosen from various regions of each town. Previous experience suggested that older middle class neighborhoods had the highest density of *A. suspensa* hosts; we chose specific quadrants that seemed on a map to match this designation. Upon arrival, we dismissed obviously unsuitable quadrants and chose others to replace them. We sampled four quadrants per town, except in LaBelle, where five quadrants were sampled. We counted host trees during a slow drive through the neighborhood, thus counting trees in backyards only

if observed from the street. Because towns differ in the size and visibility of backyard properties, the number of trees present but not observed per unit area would presumably also differ. Therefore, comparisons of towns based on number of trees counted per unit area may not be reliable. Rather, we estimated relative density as the number of trees observed per kilometer of road. Distances traveled per quadrant ranged from 4.3 to 14.8 km, but they were usually between 5 and 10 km. Results of this survey are given in Table 3.

To estimate densities of *A. suspensa*, we used McPhail trap capture data provided by the U.S. Department of Agriculture and by the Florida Department of Agriculture and Consumer Services, Division of Plant Industry (maintained at North Florida Research and Education Center, Quincy, FL). We used only trapping data from urban locations, to conform to parasitoid data that also were derived from urban sites. Data were available in the form of monthly numbers of flies per trap for various counties, but the exact identity of the town(s) where traps were situated is unknown. Following are the counties for which data

Table 2. Numbers of samples collected and mean percentage of parasitism for various host fruits at all sites combined

Host	No. samples <sup>a</sup>					Mean % parasitism ( $\pm$ SE) <sup>b</sup>		
	Total	with CFF	with Da	with Dl	with Ua	Da	Dl	Ua
Loquat	549	418	56	30	13	2.0 (0.3)Ba	1.5 (0.4)Ba	0.2 (0.1)Bb
Surinam cherry	377	326	64	55	63	7.8 (1.0)Aa	3.6 (0.6)Ab	3.0 (0.6)Ab
Cattley guava	83	60	14	15	7	7.1 (2.8)Aa	5.3 (1.6)Aab	1.1 (0.5)Bb
Common guava	290	261	52	33	4	2.5 (0.4)Ba	1.0 (0.3)Bb	0.03 (0.02)Bc

CFF, Caribbean fruit fly; Da, *Doryctobracon areolatus*; Dl, *Diachasmimorpha longicaudata*; and Ua, *Utetes anastrephae*.  
<sup>a</sup> Each sample includes fruits from a single host tree.

<sup>b</sup> Means within a column followed by the same uppercase letter, and means within a row followed by the same lowercase letter, are not significantly different ( $P < 0.05$ ; Waller–Duncan k-ratio *t*-test).

Table 3. Mean host fruit plant density (trees per kilometer of road) ( $\pm$ SE) in various towns

Town	Loquat	Surinam cherry	Cattley guava	Common guava
Arcadia	3.4 (0.4)	2.6 (0.4)	0.8 (0.1)	0.10 (0.06)
Belle Glade	2.2 (0.5)	7.7 (0.8)	0.2 (0.02)	0.5 (0.3)
Bradenton	3.3 (0.6)	4.6 (0.7)	0.3 (0.1)	0.02 (0.02)
Dade City	6.5 (0.4)	0.04 (0.04)	0	0.04 (0.04)
Ft. Lauderdale	1.8 (0.4)	5.3 (0.9)	0.5 (0.2)	0
Ft. Myers	0.9 (0.2)	2.7 (0.3)	0.6 (0.1)	0.06 (0.04)
Ft. Pierce	4.4 (0.5)	4.9 (0.9)	1.4 (0.7)	0.2 (0.1)
LaBelle	3.0 (0.8)	3.4 (0.8)	1.0 (0.2)	2.4 (0.9)
Lakeland	3.5 (1.4)	3.7 (0.4)	0	0.06 (0.04)
Lake Placid	2.9 (1.2)	4.9 (0.9)	0.5 (0.2)	0.5 (0.3)
Lake Wales	6.1 (0.6)	7.4 (0.8)	0.5 (0.2)	0.4 (0.2)
Melbourne	5.9 (1.1)	3.2 (1.0)	0.3 (0.1)	0.3 (0.1)
Miami	1.1 (0.4)	12.9 (3.9)	0.3 (0.2)	0.7 (0.3)
Naples	2.5 (0.3)	4.8 (0.3)	3.9 (1.2)	0.10 (0.06)
Okeechobee	3.1 (0.2)	3.7 (0.4)	0.5 (0.1)	0.6 (0.3)
Punta Gorda	3.9 (1.7)	4.2 (1.1)	0.3 (0.1)	0
St. Cloud	3.4 (0.6)	2.3 (0.6)	0.2 (0.1)	0.2 (0.1)
St. Petersburg	3.0 (0.2)	8.2 (2.0)	0.2 (0.1)	0.06 (0.03)
Tampa	5.8 (1.1)	2.6 (0.5)	0.2 (0.1)	0.04 (0.04)
Venice	2.4 (0.3)	2.3 (0.6)	0.6 (0.2)	0
Wauchula	4.8 (0.6)	3.5 (1.0)	0.8 (0.2)	0.8 (0.2)

were available, with the fruit collection site to which we related them in subsequent analyses in parentheses: Brevard (Melbourne), Broward (Ft. Lauderdale), Charlotte (Punta Gorda), Collier (Naples), Dade (Miami), De Soto (Arcadia), Hardee (Wauchula), Highlands (Lake Placid), Hillsborough (Tampa), Lee (Ft. Myers), Manatee (Bradenton), Okeechobee (Okeechobee), Palm Beach (Belle Glade), Pinellas (St. Petersburg), Polk (Lakeland), Sarasota (Venice), and St. Lucie (Ft. Pierce). Trapping data were from the years 1992–1996, except for Brevard, Broward, Dade, Palm Beach, and Pinellas counties, for which data were from 1990 to 1996. We calculated the mean monthly catch, minimal monthly catch and maximal monthly catch for each year, and used the mean annual value for each variable for analysis.

**Statistical Analysis.** Parasitism data were arcsine square-root transformed before analysis. We analyzed associations of environmental factors with presence or absence of each parasitoid species using logistic regression models (SAS Institute 1989), testing all temperature, precipitation, and fruit tree density factors in separate analyses.

We analyzed associations of temperature, precipitation, and host fruit tree density with parasitism levels by using multiple linear regression models. To separate effects on abundance from those on presence or absence, models included only sites in which the relevant species was collected. Data were analyzed separately for the various fruit types. Initially, all temperature, precipitation, and fruit tree density factors were included, and their relative fit with the model determined by the forward selection procedure (SAS Institute 1989). The final model included all factors significantly related with parasitism levels.

Host fly population levels are not independent of the previously described factors, i.e., temperature, precipitation, and host fruit tree density. Therefore, we could not include host fly data as factors in the

previous analyses, and we used separate linear regression models to examine relationships between fly trapping variables and parasitism levels. All sites were included in this analysis. Thus, in this case we did not differentiate between the effects of presence or absence of parasitoid species and their relative abundance.

## Results

**Distribution and Abundance of Parasitoids.** With data from all towns combined, Table 2 shows parasitism levels were higher in Surinam cherry and Cattley guava than in loquat or common guava for both *D. areolatus* and *D. longicaudata*; for *U. anastrephae*, parasitism levels were higher in Surinam cherry than in any other fruit; parasitism by *U. anastrephae* was extremely low in common guava, with only eight individuals recovered from four samples.

Overall, *D. areolatus* was more abundant than *D. longicaudata* in Surinam cherry and common guava, but not in loquat or Cattley guava (Table 2). Both species were more common than *U. anastrephae* in loquat and common guava, but mean parasitism levels of *D. longicaudata* and *U. anastrephae* were not significantly different in Surinam cherry or Cattley guava.

With all data combined, parasitism levels are low (Table 2). However, these data include sites where certain parasitoid species were totally absent from samples, and even where parasitoids were recovered, many samples did not contain parasitoids (Tables 1 and 2). Moreover, all three parasitoid species are capable of achieving high levels of parasitism: >50% parasitism was observed in certain samples at six sites for *D. areolatus*, at five sites for *D. longicaudata*, and at two sites for *U. anastrephae*. Additionally, these observations might underestimate the true parasitism levels, because the fruit may have been collected be-



Table 4. Mean percentage of parasitism ( $\pm$ SE) in loquat for various sites

Site	<i>D. areolatus</i>	<i>D. longicaudata</i>	<i>U. anastrephae</i>
Arcadia	6.6 (1.8)Aa	0CB	0Cb
Belle Glade	0B	0C	0C
Bradenton	0B	0C	0.1 (0.1)C
Dade City	0B	0C	0C
Ft. Lauderdale	0B	2.0 (2.0)BC	0.7 (0.7)C
Ft. Myers	0.2 (0.1)ABb	6.9 (1.1)ABA	1.1 (0.5)BCab
Ft. Pierce	0B	0.7 (0.6)BC	4.6 (3.3)A
Haines City	0B	0C	0C
LaBelle	4.9 (1.5)ABb	10.4 (0.3)AA	0Cc
Lakeland	0B	0C	0C
Lake Placid	3.1 (1.9)ABa	0CB	0Cb
Lake Wales	2.7 (1.4)ABa	0CB	0b
Melbourne	0B	0C	0C
Miami	0B	1.8 (1.8)BC	1.8 (1.8)B
Naples	0B	0.05 (0.05)C	0.4 (0.4)C
Okeechobee	0B	0C	0C
Punta Gorda	0.3 (0.3)AB	0C	0C
St. Cloud	0B	0C	0C
St. Petersburg	0B	0C	0C
Tampa	0.05 (0.05)B	0C	0C
Venice	0B	0C	0.06 (0.06)C
Wauchula	6.5 (1.5)ABa	0CB	0Cb
W. Palm Beach	0B	7.2 (7.2)AB	0C

Means within a column followed by the same uppercase letter, and means within a row followed by the same lowercase letter, are not significantly different ( $P < 0.05$ ; Waller–Duncan k-ratio *t*-test).

fore all *A. suspensa* larvae could be attacked. Note also that in large fruits such as common guavas, a substantial proportion of host larvae may not be vulnerable to attack because they cannot be reached by the parasitoid’s ovipositor (Sivinski 1991, López et al. 1999, Sivinski et al. 2001).

Mean levels of parasitism for the braconid parasitoids at various sites are summarized in Tables 4–7. At three northern locations, Dade City, Melbourne, and

Table 5. Mean percentage of parasitism ( $\pm$ SE) in Surinam cherry for various sites

Site	<i>D. areolatus</i>	<i>D. longicaudata</i>	<i>U. anastrephae</i>
Arcadia	25.1 (11.1)ABCa	0Bb	0.4 (0.3)Ab
Belle Glade	0Eb	12.1 (3.5)Aa	7.9 (3.3)Aa
Bradenton	0E	0.6 (0.6)B	2.4 (1.6)A
Ft. Lauderdale	0Ea	7.3 (3.2)ABa	5.1 (2.7)Aa
Ft. Myers	0.6 (0.6)Eb	3.6 (2.4)Bab	8.4 (2.8)Aa
Ft. Pierce	0Eb	0.7 (0.4)Bab	6.8 (3.4)Aa
Haines City	12.5 (12.5)CDE	0B	0A
LaBelle	35.8 (6.3)Aa	13.2 (3.5)Ab	1.4 (1.1)Ac
Lakeland	4.6 (2.2)Ea	0Bb	0Ab
Lake Placid	20.2 (6.9)BCDa	0Bb	0.07 (0.07)Ab
Lake Wales	10.1 (5.5)DEa	0Bb	0Ab
Melbourne	0E	0B	0A
Miami	0Eb	15.4 (7.2)Aa	1.8 (1.5)Ab
Naples	0.4 (0.4)E	2.7 (2.1)B	7.3 (6.6)A
Okeechobee	10.9 (5.1)DEa	0.8 (0.7)Bb	0.6 (0.6)Ab
Punta Gorda	3.5 (2.8)E	0B	2.4 (1.7)A
St. Cloud	0E	0B	3.8 (2.7)A
St. Petersburg	0E	0B	0A
Venice	0.06 (0.06)Eb	0Bb	4.6 (2.0)Aa
Wauchula	32.4 (8.9)ABa	0Bb	2.0 (1.3)Ab
W. Palm Beach	0E	3.5 (2.8)B	1.7 (1.7)A

Means within a column followed by the same uppercase letter, and means within a row followed by the same lowercase letter, are not significantly different ( $P < 0.05$ ; Waller–Duncan k-ratio *t*-test).

Table 6. Mean percentage of parasitism ( $\pm$ SE) in Cattle guava for various sites

Site	<i>D. areolatus</i>	<i>D. longicaudata</i>	<i>U. anastrephae</i>
Arcadia	79.7 (10.2)A	0	0A
Ft. Lauderdale	0D	0	0A
Ft. Myers	0.5 (0.3)Db	8.8 (3.4)a	1.2 (0.8)Ab
LaBelle	17.9 (11.9)C	5.7 (3.6)	0A
Lakeland	3.6 (3.6)D	0	0A
Lake Placid	65.8B	0	0A
Melbourne	0D	0	0A
Miami	0D	0	10.0 (10.0)A
Naples	0.6 (0.6)D	9.8 (5.3)	1.8 (1.4)A
Punta Gorda	0.3 (0.3)D	0.3 (0.3)	0A
W. Palm Beach	0D	0	0A

Means within a column followed by the same uppercase letter, and means within a row followed by the same lowercase letter, are not significantly different ( $P < 0.05$ ; Waller–Duncan k-ratio *t*-test).

St. Petersburg, no parasitoids were found (Table 1). *D. areolatus* was absent from the Atlantic coast and also was not collected at Belle Glade, St. Cloud, or Bradenton (Fig. 2). It was most common at interior locations and relatively rare along the Gulf Coast. However, distance from the coast was not a significant predictor of *D. areolatus* abundance, perhaps because of its absence at two interior locations.

*D. longicaudata* was not collected at interior locations north and west of Lake Okeechobee or at the most northern locations along both coasts (Fig. 2). It was uncommon at locations at the northern end of its distribution range (e.g., Bradenton and Okeechobee), with the exception of LaBelle. Abundance of *D. longicaudata* was significantly greater at lower latitudes in both Surinam cherry ( $F = 12.9$ ,  $P = 0.002$ ) and common guava ( $F = 6.5$ ,  $P = 0.02$ ). *U. anastrephae* was widespread and collected at most locations (Table 1). Parasitism levels for this species were relatively low, especially at most interior locations.

Table 7. Mean percentage of parasitism ( $\pm$ SE) in common guava for various sites

Site	<i>D. areolatus</i>	<i>D. longicaudata</i>	<i>U. anastrephae</i>
Arcadia	10.2 (4.1)Aa	0Bb	0Bb
Belle Glade	0B	2.0 (1.4)B	0B
Bradenton	0B	0B	0B
Dade City	0B	0B	0B
Ft. Lauderdale	0Bb	3.5 (1.7)Ba	0.2 (0.2)Bb
Ft. Myers	2.4 (2.1)AB	9.6 (4.4)A	1.0 (0.7)A
Ft. Pierce	0B	0.4B	0B
LaBelle	7.1 (2.8)ABa	3.0 (1.2)Bab	0Bb
Lakeland	2.5 (1.4)ABa	0Bb	0.03 (0.03)Bab
Lake Placid	4.9 (2.0)ABa	0Bb	0Bb
Lake Wales	4.5 (1.8)ABa	0Bb	0Bb
Melbourne	0B	0B	0B
Miami	0Bb	1.3 (0.7)Ba	0Bb
Naples	0B	4.9 (4.9)AB	0B
Okeechobee	0B	0.8 (0.8)B	0B
St. Cloud	0B	0B	0B
St. Petersburg	0B	0B	0B
Tampa	0.05 (0.05)B	0B	0B
Wauchula	6.2 (2.9)ABa	0Bb	0Bb
W. Palm Beach	0B	0B	0B

Means within a column followed by the same uppercase letter, and means within a row followed by the same lowercase letter, are not significantly different ( $P < 0.05$ ; Waller–Duncan k-ratio *t*-test).

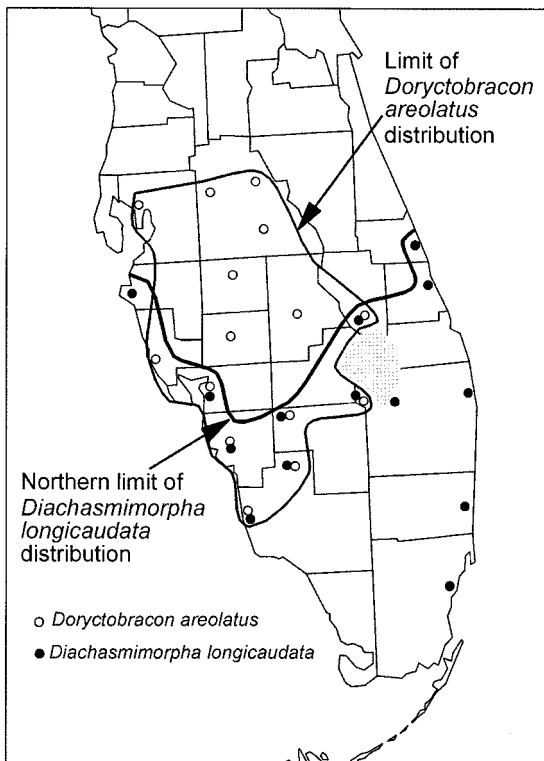


Fig. 2. Distribution of *D. areolatus* and *D. longicaudata*. Includes data from the current study and Sivinski et al. (1996).

The distribution ranges of *D. areolatus* and *D. longicaudata* overlap only within a limited area from Lake Okeechobee to the Gulf of Mexico coast (Fig. 2). In

fact, only at LaBelle were both common (Fig. 3); LaBelle was among the sites with the highest parasitism levels for both *D. areolatus* and *D. longicaudata*. With all sites included, there was no significant relationship between parasitism levels of *D. areolatus* and *D. longicaudata* in Surinam cherry (we present results of correlation analyses for this host fruit, because it is abundant, widespread, and exhibits high levels of parasitism; Spearman correlation coefficient,  $-0.27$ ;  $P = 0.23$ ). However, with LaBelle excluded, parasitism by the two species was negatively related (Spearman correlation coefficient,  $-0.48$ ;  $P = 0.034$ ).

Although *U. anastrephae* is widespread, it is most common in coastal locations and in Belle Glade, i.e., at locations where *D. areolatus* is absent or rare and where *D. longicaudata* is common. With all sites included, parasitism levels of *U. anastrephae* and *D. longicaudata* in Surinam cherry were positively related (Spearman correlation coefficient,  $0.53$ ;  $P = 0.014$ ), indicating a similar distribution pattern for both species. However, when considering only sites where both species were recovered, no significant relationship was observed (Spearman correlation coefficient,  $-0.02$ ;  $P = 0.96$ ), suggesting that they do not affect each other on a local level.

With all sites included, no significant relationship was observed between parasitism levels of *U. anastrephae* and *D. areolatus* in Surinam cherry (Spearman correlation coefficient,  $-0.35$ ;  $P = 0.12$ ). However, when only sites with both species present were considered, parasitism was negatively related (Spearman correlation coefficient,  $-0.70$ ;  $P = 0.044$ ). This suggests that *U. anastrephae* and *D. areolatus* may have a negative effect on each other, although this should be confirmed with controlled experiments.

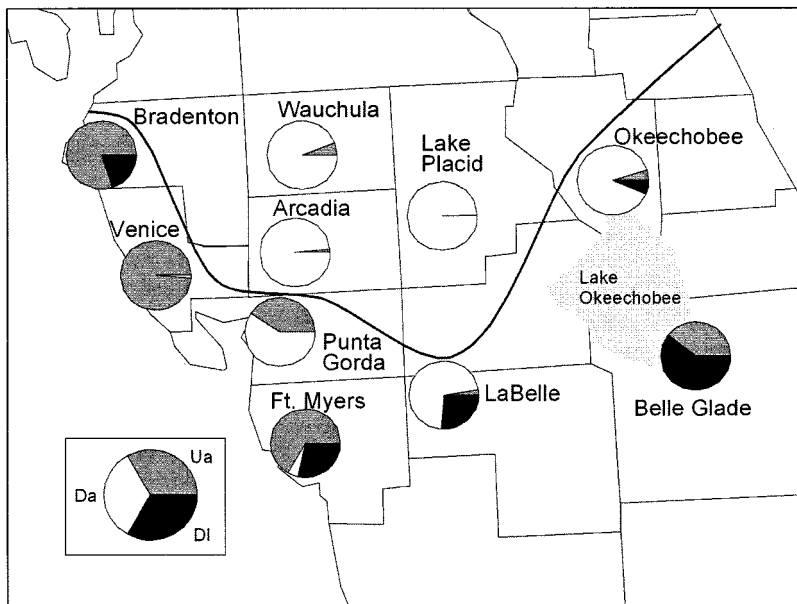


Fig. 3. Relative abundance of parasitoid species in Surinam cherry in the region of co-occurrence. Da, *D. areolatus*; Dl, *D. longicaudata*; Ua, *U. anastrephae*. The solid line represents the northern limit of distribution for *D. longicaudata*.

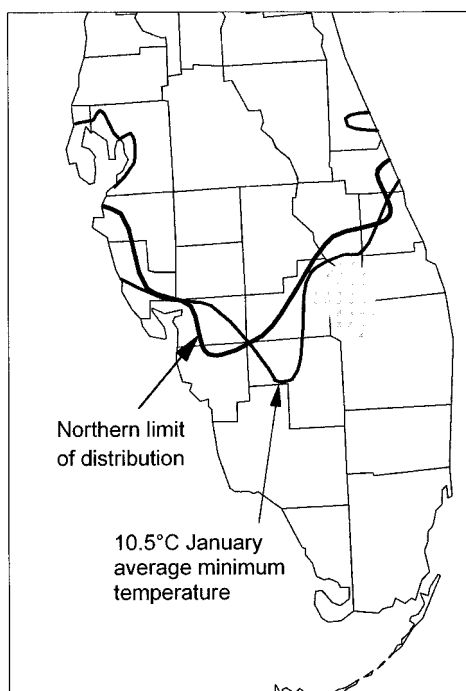


Fig. 4. Relationship between the northern observed limit of *D. longicaudata* distribution and January mean minimum temperature. The isotherm was copied from Fernald (1981), based on data from the years 1960–1979.

A fourth parasitoid, the eulophid *Aceratoneuromyia indica* Silvestri, emerged from two puparia collected from common guava at Belle Glade in February 1995. To our knowledge, this is the only report of this species outside the area of its introduction in Dade County,  $\approx 140$  km to the south.

**Relationships with Environmental Factors.** The northern limit of *D. longicaudata* distribution closely fits the isotherm of 10.5°C January mean minimum temperature (Fig. 4), i.e., it is absent from areas with low winter temperatures. The number of frost days also fits the distribution (see map in Fernald 1981), but to a lesser degree. However, mean minimum temperature for the coldest month was not a significant factor in the logistic regression analysis ( $\chi^2 = 3.51$ ,  $P = 0.061$ ). Rather, presence of this parasitoid was best explained by low variance in temperatures (four different variance factors; Table 8), i.e., relatively low seasonality. Other factors significantly related to the presence of *D. longicaudata* included mean and extreme minimum temperatures (positive relationships) and abundance of loquat trees (negative relationship). In contrast with *D. longicaudata*, variance of extreme minimum temperatures was positively related with the presence of *D. areolatus* (Table 8). The presence of *D. areolatus* also was positively associated with extreme maximum temperatures; summer temperatures are often greater at northern and inland sites than at southern and coastal locations. The presence of *U. anastrephae* showed no significant relationships with

Table 8. Environmental factors significantly associated with presence or absence of parasitoid species, according to logistic regression analysis

Parasitoid species	Factor (relationship) <sup>a</sup>	$\chi^2$	P
<i>D. areolatus</i>	Var extreme min temp (+)	4.26	0.039
	Extreme max temp (+)	4.00	0.045
<i>D. longicaudata</i>	Var extreme max temp (–)	5.79	0.016
	Var extreme min temp (–)	5.69	0.017
	Var mean max temp (–)	4.82	0.028
	Var mean temp (–)	4.70	0.030
	Mean temp (+)	4.46	0.035
	Extreme min temp (+)	4.28	0.038
<i>U. anastrephae</i>	Loquat density (–)	4.25	0.039
	Loquat density (–)	5.78	0.016

<sup>a</sup> Extreme maximum (max) temperature, extreme maximum annual temperature; Extreme minimum (min) temp, extreme minimum annual temperature; Loquat density, mean density of loquat trees; Var extreme max temp, variance of monthly extreme maximum temperatures; Var extreme min temp, variance of monthly extreme minimum temperatures; Var mean max temp, variance of monthly mean maximum temperatures; Var mean temp, variance of monthly mean temperatures.

abiotic factors, but it was negatively related with abundance of loquat trees (Table 8).

Table 9 details the statistically significant relationships between abiotic and host fruit tree density factors and parasitoid abundance. *D. areolatus* was more common at sites with lower mean temperatures, in both Surinam cherry and Cattley guava. Similarly, parasitism levels in common guava were negatively associated with extreme minimum temperatures. Variance of extreme maximum temperatures was negatively related with *D. longicaudata* abundance in Surinam cherry. Variance of precipitation was positively associated with *D. areolatus* abundance in Cattley and common guava, and with *D. longicaudata* abundance in loquat.

Guava tree density was significantly associated with parasitism levels of both *D. areolatus* (positive relationship in Surinam cherry) and *D. longicaudata* (positive relationships in loquat and Surinam cherry) (Table 9). Loquat tree density was negatively related with *D. longicaudata* parasitism levels in Surinam cherry and common guava. Similarly, Surinam cherry tree density was negatively related with *D. longicaudata* abundance in common guava. A positive relationship was observed between Surinam cherry tree density and parasitism levels of *U. anastrephae* in Cattley guava. There were no significant relationships between tree density and parasitism on the same host.

There were statistically significant positive relationships between *A. suspensa* density and parasitism by *D. longicaudata* in loquat (minimum monthly capture of host flies;  $R^2 = 0.64$ ,  $P < 0.001$ ) and common guava (mean monthly capture of host flies,  $R^2 = 0.68$ ,  $P < 0.001$ ), and between minimal monthly capture of *A. suspensa* and parasitism by *U. anastrephae* in loquat and Surinam cherry ( $R^2 = 0.38$ ,  $P < 0.01$ ;  $R^2 = 0.30$ ,  $P < 0.05$ , respectively). No statistically significant relationships were found between fly trapping variables and parasitism by *D. areolatus*.



Table 9. Environmental factors significantly associated with parasitism levels, according to multiple linear regression analysis

Parasitoid species	Host fruit	Factor (relationship) <sup>a</sup>	Model R <sup>2</sup>
<i>D. areolatus</i>	Surinam cherry	Guava density (+)**	0.81
		Mean temp (-)**	
	Cattley guava	Mean temp (-)***	0.98
		Var precipitation (+)**	
	Common guava	Extreme min temp (-)***	0.84
<i>D. longicaudata</i>	Loquat	Var precipitation (+)**	
		Guava density (+)*	0.68
	Surinam cherry	Var precipitation (+)*	
		Guava density (+)***	0.87
		Loquat density (-)**	
	Common guava	Var extreme max temp (-)**	
		Loquat density (-)*	0.75
		Surinam cherry density (-)*	
	Cattley guava	Surinam cherry density (+)**	0.68

<sup>a</sup>Extreme minimum (min) temp, extreme annual min temp; Guava density, mean density of common guava trees; Loquat density, mean density of loquat trees; Mean temp, mean annual temp; Surinam cherry density, mean density of Surinam cherry trees; Var extreme maximum (max) temp, variance of the monthly extreme max temperatures; Var precipitation, variance of the monthly precipitation. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

### Discussion

One of the primary findings of this study is the total absence of *D. longicaudata* from the interior region of central Florida. Results indicate a negative relationship between the distribution of *D. longicaudata* and the variance of monthly temperatures, suggesting that this species may be dependent on a relatively constant supply of hosts. This conclusion is supported by significant relationships between the abundances of *A. suspensa* and *D. longicaudata* (but not *D. areolatus*). In Mexico, *D. longicaudata* tended to become relatively rare at high altitudes in sour orange, *Citrus aurantium* L., but increased with altitude in common guava (Sivinski et al. 2000), suggesting that both biotic and abiotic factors are important in its distribution.

Diapause development is an important mechanism allowing insects to cope with periods of low host availability. There is evidence that *D. longicaudata* individuals do indeed enter diapause (Clausen et al. 1965, Ashley et al. 1976, Aluja et al. 1998, Eitam 1998). However, in Mexican populations both the proportion of individuals entering diapause and the length of diapause period are greater for *D. areolatus* than for *D. longicaudata* (Aluja et al. 1998). Additionally, Aluja et al. (1998) reported circumstantial evidence that *D. areolatus* adults may enter a reproductive diapause. These observations suggest that *D. longicaudata* may be less adapted than *D. areolatus* to survive long periods without hosts.

We cannot, however, reject the possibility of direct effects of temperature on *D. longicaudata* distribution, just as winter temperatures may have limited the establishment of *F. arisanus* in Australia (Snowball and Lukins 1964, Snowball 1966). Sivinski et al. (1998) report a reduction in the abundance of *D. longicaudata* relative to that of *D. areolatus* in calamundin, *Citrofortunella mitis* J. Ingram & H.E. Moore, at LaBelle during winter, suggesting some climatic effect unrelated to host availability. Laboratory studies suggest that *D. longicaudata* may be less tolerant to low temperatures than its host *A. suspensa* (Eitam 1998). Fur-

ther studies are needed to determine whether its tolerance is lower than that of *D. areolatus*.

Our second primary finding is the absence of *D. areolatus* from coastal southern Florida, the very region in which it was established >30 yr ago (Baranowski and Swanson 1970). In Mexico, relative abundance of *D. areolatus* is negatively related with altitude (Sivinski et al. 2000), suggesting that its distribution in Florida is not the result of preference for, or adaptation to, low temperatures. Rather, the current distribution pattern suggests that competition by *D. longicaudata* may have caused its displacement.

Similar cases involving fruit fly parasitoids in Hawaii are considered among the classic examples of apparent competitive displacement. In the first case, *Psytalia* (formerly *Opius*) *humilis* (Silvestri) was replaced by *Diachasmimorpha tryoni* (Cameron) as the dominant parasitoid of the Mediterranean fruit fly, *Ceratitis capitata* (Weidemann) (Pemberton and Willard 1918). Note, however, that numbers of *P. humilis* subsequently increased, and by 1933 *P. humilis* and *D. tryoni* provided equivalent levels of parasitism (Willard and Mason 1937). In the second occurrence, several parasitoid species were released during the late 1940s for the control of *B. dorsalis* (Clausen et al. 1965). Initially, *D. longicaudata* was the dominant species, only to be replaced by *Fopius* (formerly *Biosteres*) *vandenboschi* (Fullaway), which was in turn replaced by *Fopius* (formerly *Biosteres*) *arisanus* (Sonan) (van den Bosch et al. 1951).

*D. areolatus* and *D. longicaudata* are of similar size, and both have relatively long ovipositors (Sivinski et al. 1997). They also show similar preferences for host fruits (Table 2), do not differ in their microhabitat preferences within host tree canopies (Sivinski et al. 1999), and both attack second and third instars (Lawrence et al. 1976, Eitam et al. 2003). Thus, the potential for competition between these species is obvious. The interaction between them is a new association, because *D. areolatus* is a Neotropical species, whereas *D. longicaudata* originates in the Indo-Pacific region

(Clausen 1978). Therefore, they would not have evolved niche divergence to avoid competition with each other.

Possible mechanisms for a competitive advantage of *D. longicaudata* over *D. areolatus* include an advantage in locating fruits containing host larvae, or in locating larvae within fruits, higher fecundity, or superiority in larval competition. Further studies are needed to fully explore these possibilities. Perhaps the most obvious advantage of *D. longicaudata* over *D. areolatus* is its longer ovipositor, enabling it to reach larvae deeper within fruits, thus allowing access to a larger proportion of larvae, especially in large fruits (Sivinski et al. 1997, 2001).

Studies suggest that *D. longicaudata* may have a competitive advantage over other species in situations of multiparasitism [but see van den Bosch and Haramoto (1953) for opposing evidence]. Palacio et al. (1991) found that *D. longicaudata* was a superior competitor to both *F. arisanus* and *Fopius* (formerly *Bio-steres*) *persulcatus* (Silvestri), indicating physical competition among first instars. Studies by Bautista and Harris (1997) with *D. longicaudata* and *Psytalia incisi* (Silvestri) indicate that the sequence of oviposition is important, with the first parasitoid species to oviposit in the host having an advantage. However, whereas exposure first to *P. incisi* resulted in 77% of the progeny being of this species, the reverse sequence resulted in 99% of the progeny being *D. longicaudata*.

Sivinski et al. (1998) hypothesized that the co-occurrence of *D. longicaudata* and *D. areolatus* at LaBelle may be the result of "counterbalanced competition" (Zwölfer 1971) where *D. areolatus* is superior to *D. longicaudata* in locating host patches (=extrinsic competitor) and *D. longicaudata* is superior in exploiting these patches (=intrinsic competitor). Applying this hypothesis to a large geographic scale, the better searcher would be at an advantage at locations that have a less predictable supply of hosts in time or space, whereas the better intrinsic competitor would benefit from more homogeneous host availability. In the more northern interior regions of Florida, where temperatures are more variable, large gaps may occur between fruiting cycles of the various hosts, and in particular between the fall fruiting of guava and the spring fruiting of loquat. At coastal locations where temperature conditions are more homogeneous, trees may have more than one fruiting cycle, filling in the temporal gaps in fruit availability (Nguyen et al. 1992). Furthermore, additional tropical host fruits occur in the southern coastal regions (Hennessey 1994). The former conditions (greater seasonality, less homogeneous host distribution) would favor the superior searcher, presumably *D. areolatus*, whereas the latter (less seasonality, more homogeneous host distribution) would benefit the superior intrinsic competitor, i.e., *D. longicaudata*. In extreme conditions, one parasitoid species may be driven to extinction and at intermediate locations both would persist.

This hypothesis is supported by studies of parasitoid distribution in the tropics. In these regions, native habitat is heterogeneous in host availability, favoring

a superior searcher, whereas there is a more predictable supply of hosts in cultivated or urban areas, favoring a superior intrinsic competitor. In Mexico, *D. longicaudata* is the dominant species in an area of mixed cultivation, whereas it is absent in native habitats where *D. areolatus* is most common (Aluja et al. 1990, Hernandez-Ortiz et al. 1994). Similarly, in Amazonas State, Brazil, *D. areolatus* is the dominant parasitoid in rural locations, whereas *Opius* sp. nr. *bellus* is dominant in urban areas (Canal et al. 1995). In the tropics, the presence of wild hosts may give *D. areolatus* refuge from competition, thus preventing displacement. Such a refuge does not exist in Florida, where most hosts are in either urban or agricultural habitats.

The biology of *U. anastrephae* is little known, and its interactions with other parasitoid species are unclear. In Mexico, Sivinski et al. (1997) observed negative relationships between *U. anastrephae* and *D. areolatus* within tree canopies. This was interpreted as being the possible result of evolution of divergent niches in these sympatric species, which would reduce direct competition. However, the inverse among-site relationship observed between these two species in this study suggests that significant within-site competition may be occurring. *U. anastrephae* is common only in small fruits such as Surinam cherry (Table 5); thus, significant competition would occur only in such fruits. Because *D. areolatus* was established in Florida with *U. anastrephae* already present, it seems that competition by *U. anastrephae* alone is not highly significant. However, *U. anastrephae* occurs in large numbers in most of the same towns where *D. longicaudata* is common (Fig. 3). Thus, coupled with the competitive pressure of *D. longicaudata*, it may have contributed to the displacement of *D. areolatus*. Alternatively, *U. anastrephae* may be common at these locations because *D. longicaudata* had suppressed *D. areolatus*, thus releasing the former species from competition.

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